Shifts in food plant abundance for flower-visiting insects between 1900 and 2017 in the canton of Zurich, Switzerland

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Shifts in food plant abundance for flower-visiting insects between 1900 and 2017 in the canton of Zurich, Switzerland

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Abstract. Adult flower-visiting insects feed on nectar and pollen and partly collect floral resources to feed their larvae. The reduction in food availability has therefore been proposed as one of the main causes for the drastic decline in flower-visiting insects in Central Europe. We compared the current (2012–2017) abundances of food plants of different groups of flower-visiting insects to that of 1900–1930 in the canton of Zurich, Switzerland. Comparisons were done separately for different vegetation types, flowering months, and groups of diurnal flower-visiting insects, such as bees, bumble bees, wasps, butterflies, hoverflies, flies, and beetles. We found a general decrease in food plant abundance for all groups of flower-visiting insects and in all vegetation types except ruderal areas. Reductions of food plant abundance were most pronounced for wetlands and agricultural fields, reflecting the massive transformation of wetlands into other habitat types and the intensified management of agricultural fields. Food plant abundance for specialized flower visitors (bees, bumble bees, butterflies) of wetlands decreased most strongly in May and for generalized flower visitors (wasps, hoverflies, flies, beetles) in July. Specialized plant species, i.e., species with few groups of flower visitors, decreased more strongly in abundance than species with many groups of flower visitors. Finally, we found a homogenization of food plant assemblages in all vegetation types except ruderal areas, where the opposite pattern emerged. Our results suggest a significant reduction in the diversity and abundance of food plants for flower-visiting insects over the past century, which has been most severe for the more specialized insect groups. The trend of insect decline, in particular those specialized on few plant species, can only be stopped by extending suitable habitats, i.e., by increasing food availability and reestablish selected plant populations.

Key words: *bees; beetles; butterflies; flower visitors; homogenization; hoverflies; land-use change; phenology; pollination; specialization; wasps.*

Introduction

In the last few years, the drastic worldwide decline of insects has become prominent in both the scientific and the public domain (Biesmeijer et al. 2006, de Palma et al. 2016, Hallmann et al. 2017). In some regions of Europe, the biomass and abundance of insects has decreased by ≤82% over the past years (Hallmann et al. 2017, Seibold et al. 2019), while the local diversity of individual insect groups, such as bees and hoverflies, has dropped by up to 60% since World War II (Biesmeijer et al. 2006). As a result, about 50% of the species of major insect groups, such as bees and butterflies, are listed as threatened by extinction in many European countries (Fitzpatrick et al. 2006, Cordillot and Klaus 2011, Westrich et al., 2011). These enormous reductions in insect diversity and abundance put ecosystem functions, such as pollination of wild plants and crops, at risk (Potts et al. 2010).

One of the most important reasons for the decline of insects is habitat loss due to land-use change, especially the conversion of flower-rich, extensively used pastures, hay meadows, and wetlands into intensively used meadows and agricultural fields, and the conversion of seminatural habitats into urban land (Nilsson et al. 2008, Ollerton et al. 2014, de Palma et al. 2016). Additionally, the massive application of fertilizers and pesticides in agriculture has strongly reduced insect diversity (Brittain et al. 2010). These changes in management have also led to a decrease in the abundance of flowers, which provide essential food sources (mostly nectar and pollen) for various groups of insects (Carvell et al. 2006, Fitzpatrick et al. 2007, Nilsson et al. 2008, Bates et al. 2011, Wallisdevries et al. 2012, Scheper et al. 2014). Not only the

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abundance of flowers but also the diversity and composition of flowering plant assemblages determine the diversity and abundance of insects (Potts et al. 2003, Grundel et al. 2010, Bruckman and Campbell 2014). Some groups, such as oligolectic bees, depend on a narrow range of food plant species, whereas the majority of flower-visiting insects use a wide range of food plant species. Nevertheless, polylectic insect species are also morphologically and phenologically adapted to a subset of all available food plant species and need a continuously large supply of high-quality nectar and pollen (Goulson et al. 2008). However, the protein content of pollen varies drastically between plant species. Wind-pollinated species such as maize tend to have very low pollen protein content, representing poor pollen quality for bees, although they still frequently collect the abundant pollen (T'ai et al. 2000). The general homogenization and reduction of wild and domestic plant and flower diversity in today's landscapes therefore have a negative impact on all groups of flower-visiting insects, and in particular on more specialized groups, such as bees, bumble bees, and butterflies (Fründ et al. 2010, Weiner et al, 2011, Carvalheiro et al. 2013).

Despite the obvious importance of food plants for insects, surprisingly little is known about how long-term spatial and temporal changes in food plant abundance influence flower-visiting insects at the landscape scale (Moroń et al. 2008, Scheper et al. 2014, Baude et al. 2016). Some studies indicate that in agricultural habitats, a phenological change in the diversity patterns of flower-visiting insects corresponds to a change in flower abundance (Oertli et al. 2005, Leong et al. 2016). However, the variation in food plant abundance in different vegetation types has not been quantitatively compared over time spans of several decades. This lack of research is largely caused by the difficulty of obtaining historical baseline data on flower availability.

In the current study, we take advantage of a recent citizen science project mapping the historical and current distributions of all wild plant species of the canton of Zurich, Switzerland (Wohlgemuth et al. 2020). Our data comprise information on plant species abundances for the periods 1900–1930 and 2000–2017. Based on this information we analyze changes in the abundance and diversity of food plant species for seven groups of flower-visiting insects in six different habitat types and in different flowering seasons. Specifically, we asked (1) How has the abundance of food plants changed for flower-visiting insects in specific habitats and different flowering periods during the last 100 yr? (2) Have the abundances of food plant species of specialized and generalized insects decreased differently? (3) Does the decrease of plant species with few groups of flower-visiting insects differ from that of plant species with many groups of flower-visiting insects? (4) Was there a homogenization of food plant assemblages in the different habitat types during the last 100 yr?

Materials and Methods

Study area

Current distributions and abundances of plant species were assessed within the citizen science project Flora of the Canton of Zurich (FloZ), to which about 250, well-trained volunteers contributed observational data between 2012 and 2017 (Wohlgemuth et al. 2020). The canton of Zurich, situated in northern Switzerland in the foothills of the northern Pre-Alps and the Swiss Central Plateau, has an area of 1,729 km^2. Corresponding to the elevational range between 330 and 1,292 m above sea level, natural vegetation types are colline and montane mixed broad-leaved forests, often dominated by European beech (*Fagus sylvatica* L.), meadows, bogs, and lake vegetation. However, large parts of the canton were converted to agricultural and urban land. The proportions of land-use types have strongly changed during the last 100 yr. Especially prominent was the reduction of agricultural land (from 63% to 41.4% cover) in favor of urban land (from 3.6% to 21.6% cover) while the proportion of forest remained relatively constant (from 27% to 30.6% cover; Wohlgemuth et al. 2020). The most drastic loss (by ~90%) concerned wetlands, which were mostly drained and transformed to agricultural land, mostly intensively used grassland (Gimmi et al. 2011, Wohlgemuth et al. 2020).

Categorization of the current and historical abundance of plant species

For the assessment of the distribution of plant species, the area of the canton was subdivided into a regular grid of 257 squares each 3 × 3 km in area, containing nine cells of 1 × 1 km each. The presence of all vascular plant species in each of the central 1-km^2 cells was recorded in the field. Sampling followed a fixed protocol requiring at least three visits per cell (one each in spring, summer, and autumn) over two years. For each cell, a group of two to four experienced botanists spent about 40–60 h in the field and listed all species within the 1-km^2 area. Rare and difficult-to-identify species were documented with photos and/or by herbarium specimens for identification, with samples deposited in the United Herbaria Z/ZT. The total number of records was 103,496. Species abundances were estimated for each 1-km^2 cell in four broad categories: 1, 1–25 individuals; 2, 26–100 individuals; 3, 101–1,000 individuals; and 4, >1,000 individuals. This classification represents a compromise between detail and recording speed (it would have been impossible to count all individuals of all species in an area of 1 km^2), and it also addresses the difficulty of identifying individuals of clonal species. Because the central cell did not include all species of the 3 × 3 km square, we further included additional species records from Info Flora, the national data and information center on the Swiss Flora, regarding each 3 × 3 km

square, totaling 60,106 species records (data *available online*).[5]

To integrate the sampling data into a single index of the canton-wide abundance of each species, we took into account both the frequency (number of 1-km^2 cells with records) and the mean abundance of the species in the cells in which it was recorded (ranging from 1 to 4). By dividing the mean square abundance by the total number of squares (210) we formed five abundance categories: H1 (very rare), <0.05; H2 (rare), 0.05–0.25; H3 (locally common), 0.251–1.5; H4 (common), 1.51–2.5; and H5 (very common), >2.5. We used this fairly coarse approach because it would have been impossible to apply a finer or more spatially explicit categorization for the historical data.

For the historical canton-wide abundance categorization, we digitized information from a variety of sources. The main source was the unpublished manuscript of the flora of the canton of Zurich by Baumann (1933), which includes exact and detailed information on the distribution/occurrence of plant species recorded before 1930. In the handwritten 1,200 pages, abundances for common and widespread species were noted in general terms, and localities of findings were listed for rare species (naturally rare and spreading alien species). Other historical sources served for selected plant groups, including the records by Naegeli and Thellung (1905) and some 18,000 herbarium specimens from the United Herbaria of the University and ETH Zürich, Z/ZT. In total, locality information of 45,216 records was digitized and georeferenced by a team of trained volunteers. On the basis of all available information on the historical species presence and abundance, a group of five experts of the flora of the canton of Zurich assigned each species to one of the five canton-wide abundance categories applying the same approach as for the current data.

A plant species was defined as having changed its abundance if there was a shift in abundance category between the historical and current categorization. We acknowledge that this is a fairly rough definition, but, it is conservative in that category shifts generally correspond to declines or increases of >50% in total population size, thus excluding minor abundance shifts that would apply to essentially all species but that are impossible to quantify with the less extensive historical data.

Because our categorization is broad, we are confident that any researcher dealing with these data would arrive at a quite similar species assignment to the categories and that the patterns uncovered are robust. If we have a concern, it is that our categorization approach might have led to a loss of detailed information, potentially obscuring additional patterns. For this reason, we base our interpretations on the documented patterns, while being careful to interpret the lack of patterns.

Additionally, we assessed the sensitivity of our results by comparing our classification of species into abundance classes with an alternative classification. We reclassified the species as follows: the assignment of the species was originally conducted by five experts (M. Kessler, M. Nobis, T. Wohlgemuth, C. del Fabbro, A. Keel). For the consensus classification on which the main analyses are based, the experts discussed discrepancies between the assignments until a consensus was reached. To quantify the discrepancies, we performed a sensitivity analysis using an alternative species assignment composed by reclassified species for which at least one expert had a different opinion. This alternative classification differed from the consensus classification the most possible.

Plant traits

For 966 plant species (representing 56.2% of the 1719 seed plant species occurring in the canton of Zurich), we assigned data on groups of diurnal flower visitors based on literature (Appendix S1: Table S1), mostly from Knuth (1899, 1904) and Jäger (2011). We included more specialized (bee, bumble bee, butterfly) and more generalized groups (wasp, hoverfly, fly, beetle). If no information on flower visitors was provided in these books, we conducted a literature search in Google Scholar, entering the name of the species in combination with "pollinator" as search terms. Of the remaining seed plant species in the canton of Zurich, 393 (22.2%) are only pollinated by wind or water. For the last 360 species (21.6%) no information on flower visitors was available. Despite this intensive search, we had to exclude night-active butterflies from our analyses due to a lack of available data. We focused on flower-visiting insects instead of pollinating insects because we were interested in changes in food availability for insects. Further, pollination efficiency of individual insect groups is known for relatively few plant species.

We collected data on flowering phenology (in months) from Lauber et al. (2018) for 96% of the seed plant species occurring in the canton of Zurich. For 91% of the species, we used information on their main occurrence in vegetation types (wetland, meadow, agricultural field, shrubbery, forest, or ruderal area) from Delarze et al. (2015; information *available online*).[6] Both data sets were designed for the Swiss flora and thus have a regional basis. Additionally, we created a category for plant species of nutrient-poor meadows by excluding all meadow species occurring in artificial lawns (category 4.0 of Delarze et al. 2015), fertilized meadows (category 4.5), and grass fallows (category 4.6) to test whether the results for meadows are mainly driven by the species occurring in nutrient-rich meadows.

Statistical analyses

All analyses were conducted in R version 3.4.3 (R Development Core Team 2017). To analyze the changes

[5] www.infoflora.ch

[6] www.infoflora.ch

in food plant abundance for the individual groups of flower visitors regarding historical and present flora states, we applied Fisher's exact tests on these abundances. We conducted all analyses separately for plant species visited by the individual groups of flower visitors and considered the species' habitat type and flowering period by month. Therefore, the same plant species can be analysed more than once if it is visited by several groups of flower visitors or occurs in different vegetation types. To adjust for the large number of tests, we applied Holm corrections for the *P* values of the frequency analyses: monthly *P* values for the six main vegetation types were categorized by taxonomic groups of flower visitors and only values for the main flowering season (April–September) were considered. Thus, Holm corrections were applied to groups of 36 *P* values. To visualize our results we summed the positive and negative changes in frequency categories for each group of food plants (separated by groups of flower visitors, vegetation type, and month of flowering). To assess the sensitivity of our results, we repeated the analyses of the changes in food plant abundance for the individual groups of flower visitors per vegetation type and month by Fisher's exact tests with the re-classified data.

For each vegetation type we counted the plant species that are visited by insects of one, two, three, four, five, or six or more insect groups. Within each of these categories, we counted the species that decreased in abundance (changed from a higher to a lower abundance category) and divided this number by the total number of species within the category. For each vegetation type, we then assessed the Spearman correlation between these ratios and the number of flower-visitor groups. To evaluate whether the distribution between vegetation types differs significantly for plant species with a large or a small number of flower-visitor groups, we counted the number of plant species visited by insects belonging to one, two, three, four, five, or six or more insect groups separately for each vegetation type. Then, we compared by Fisher's exact tests per number of flower-visitor group the frequencies of species in the individual vegetation type with the frequencies of all plant species that are visited by insects in this vegetation type. Additionally, we used Fisher's exact tests within the historical data alone to determine whether frequencies in abundance categories between plant species visited by one, two, three, four, five, or six or more insect groups each differed significantly from the frequencies in abundance categories of all species that are visited by insects.

To analyze the homogenization of the flora in the canton of Zurich, we counted the abundant species (belonging to the categories very common, common, and locally common) and the infrequent species (belonging to the categories rare, very rare, and extinct before 2000), visited by different groups of insects in the different vegetation types. We then compared the historical and current numbers of species visited by the different groups of insects per vegetation type separately for the abundant and infrequent species using paired Wilcoxon tests.

Results

Of the 966 plant species visited by diurnal insect pollinators, for which we obtained data from the canton of Zurich over the last century, 927 were present in 1900–1930, with 249 (26.9%) categorized as very rare, 219 (23.6%) as rare, 275 (29.7%) as locally common, 127 (13.7%) as common, and 57 (6.2%) as very common (Fig. 1). In 2000–2017, there were 921 species in total, with 289 (32.4%) being very rare, 214 (23.2%) rare, 266 (28.9%) locally common, 92 (10.0%) common, and 60 (6.5%) very common. Of the species present in 1900–1930, 45 (4.7%) were no longer recorded in 2000–2017, while 236 (24.4%) were assigned to a lower abundance category, 143 (14.8%) were assigned to a higher category, and 542 (56.1%) remained in the same category (Fig. 1). Of the species recorded in 2000–2017, 37 (4.0%) were not documented in the canton in 1900–1930.

In all vegetation types except ruderal areas, we documented a general decrease in food plant abundance for all groups of flower visitors (Fig. 2). We found significant reductions in food plant abundances for specialized groups of flower visitors (bumble bees, bees, and butterflies) as well as for more generalized groups (e.g., hoverflies and flies), especially in wetlands and agricultural fields (Appendix S1: Table S2). For bumble bees, we

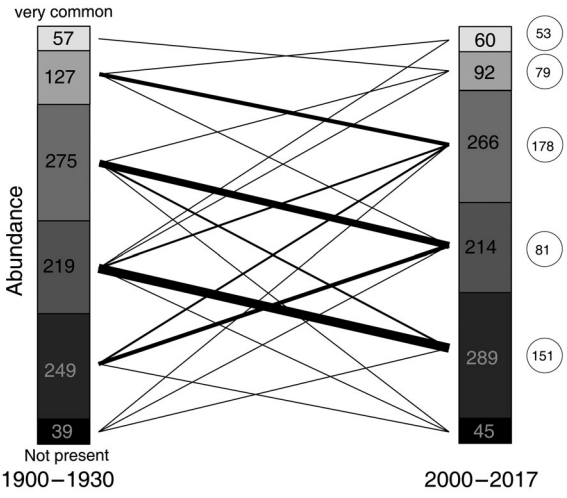

Fig. 1. Directionality of category changes between historical and current species abundances of flowering plant species visited by insects in the canton of Zurich. The thickness of the lines represents the number of changes that occurred. Numbers in boxes indicate the species number of the different abundance categories. The number of species that did not change frequency category between historical and current records is given on the right in circles. The abundance category "not present" in the historical bar (1900–1930) mostly includes neophytic species that appeared after 1930. In the current bar (2000–2017), this category mainly contains plant species that went extinct before 2000.

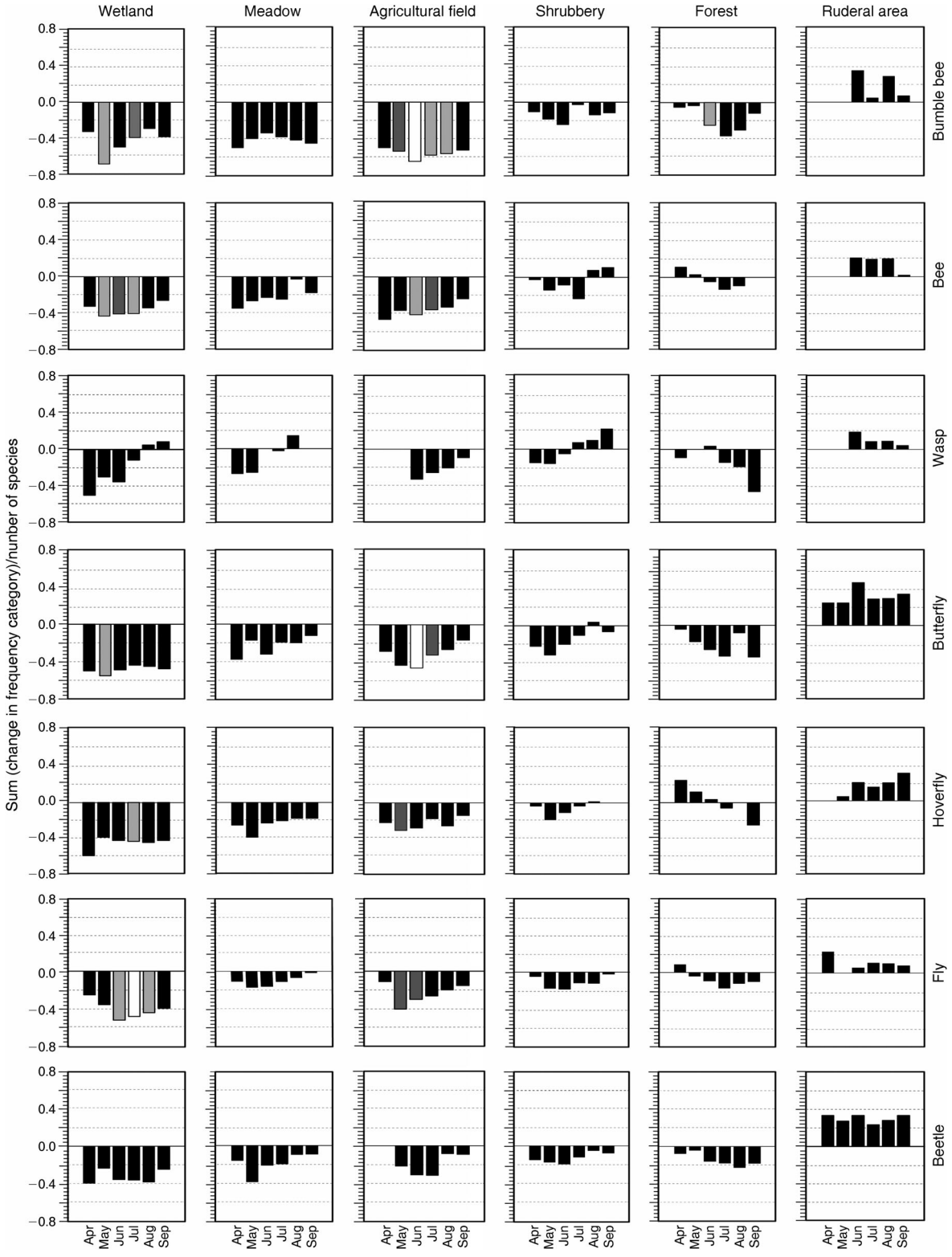

FIG. 2. Average changes in frequency categories for each group of food plants, separated by flower-visitor group, vegetation type, and month of flowering. The graphs for nutrient-poor meadows are not shown because they are largely redundant with those for meadows. Comparisons of frequencies between historic and current data were done by Fisher's exact tests (Appendix S1: Table S2). Black bars show nonsignificant changes ($P \geq 0.1$), dark gray bars show tendencies ($0.05 \leq P < 0.1$), light gray bars show significant changes ($P < 0.05$), white bars show significant changes after Holm correction.

additionally detected a significant reduction in food plant abundance in forests. Some of these reductions in food plant abundances remained significant after Holm correction, e.g., for bumble bees and butterflies in agricultural fields and flies in wetlands. Comparing abundance changes in food plants for all meadow species with those occurring only in nutrient-poor meadows, we largely found the same nonsignificant results, except regarding the food plants of butterflies with marginally significant reductions in nutrient-poor meadows (Appendix S1: Table S2). Comparing the consensus and alternative classifications, 19.1% of species were placed in a different abundance category. Using the alternative classification for the analyses, we obtained qualitatively similar results, with 94% of the results being in the same significance category (Appendix S1: Table S3), which indicates that the results are robust against the unavoidable subjective element of the classification system used. Twelve of the 15 results with differing significance categories were increases in significance, showing that the original approach was more conservative. Due to the robustness of our results, we will not further discus this topic.

Significant decreases in food plant abundances were confined in the period from May to August, but with different phenological profiles between vegetation types and groups of flower visitors (Fig. 2). In wetlands, the decrease in food plant abundances was most pronounced in May for specialized groups (bees, bumble bees, and butterflies), whereas the largest decrease in food plants for generalized groups (flies and hoverflies) was in July. In agricultural fields, the decrease in food plant abundances peaked in June for the majority of insect groups (Fig. 2).

In all vegetation types, the correlations of plant species with one, two, three, etc. groups of flower visitors against the proportion of species that changed in abundance per group of flower-visitor number revealed a negative trend (Fig. 3). This trend was significant for meadows and agricultural fields, and marginally significant for shrubbery. The distribution in species number between vegetation types was not significantly shifted for any group of species with different numbers of flower-visitor groups compared to the entire data set (Appendix S1: Tables S4–S6). However, in the historical data, plant species visited by one or two groups of flower-visiting insects were significantly rarer than expected by chance compared to the entire historical data set, whereas species visited by six or more groups of flower-visiting insects were significantly more common than expected by chance (Appendix S1: Table S4).

Through our analysis of the homogenization of the flora in the canton of Zurich in the different vegetation types, we detected a significant decrease in the number of abundant plant species (very common, common, and locally common) in the current data for all vegetation types except ruderal areas, where we found a significant pattern in the opposite direction (Fig. 4, Appendix S1: Table S7). Applying the same approach for the infrequent (rare, very rare, and extinct) plant species revealed a significant increase in the number of species for all vegetation types except ruderal areas, where we found a significant decrease in the number of species (Appendix S1: Table S7). This means that a smaller proportion of species remained abundant, whereas the large majority of species became less frequent, revealing a homogenization of plant assemblages.

Discussion

In our study, we quantitatively compared plant abundance data from the canton of Zurich retrieved from two data sets that were compiled from periods lying 100 yr apart. Being aware of the limitation of the quantitative approach underlying, we consider regional-scale comparisons crucial to understand the landscape dynamics of plant diversity. Such investigations of regional changes of plant diversity and assemblage composition over one or two centuries are much rarer than local scale studies, resampling previous vegetation surveys (Willis et al. 2008, Damschen et al. 2010). Further, most regional studies only quantified losses and gains of species rather than considering changes in abundances (Hautekèete et al. 2015). Our study profits from two floristic inventories that are both exceptional in their depth and coverage for their respective times. We used data of an unpublished flora project in the canton of Zurich covering first three decades of the 20th century, along with extensive herbarium records, to obtain over 45,000 species records for this period and compared these data with the current situation, which was assessed based on over 170,000 records. To account for this challenge, we adopted a broad categorization approach of species abundances that can be applied to both data sets. We found that during the last 100 yr the average abundances of food plant species for all groups of flower-visiting insects decreased in all vegetation types, except ruderal areas, in the canton of Zurich (Fig. 2). This trend reflects the well-known intensification in agriculture and a general urbanization in Switzerland (Bosshard 2016) and other parts of Europe (Price et al. 2015, van Vliet et al. 2015). As a consequence of urbanization, ruderal areas have increased in all parts of the canton (Wohlgemuth et al. 2020), as did the abundances of ruderal plant species. The typical ruderal flora can, however, only provide food for quite unspecialized flower-visiting insect fauna from various taxonomic groups (Bates et al. 2011, Cordillot and Klaus 2011).

Reductions in food plant abundances were most prominent in agricultural fields for more specialized groups of flower visitors, such as bees, bumble bees, and butterflies, but these changes were not significant for generalized groups of flower visitors, such as flies and beetles (Fig. 2). This difference may be explained by the relative rareness of plant species visited by more specialized flower visitors in this vegetation type. These plant species are likely more affected by management changes, in particular the application of fertilizers and pesticides

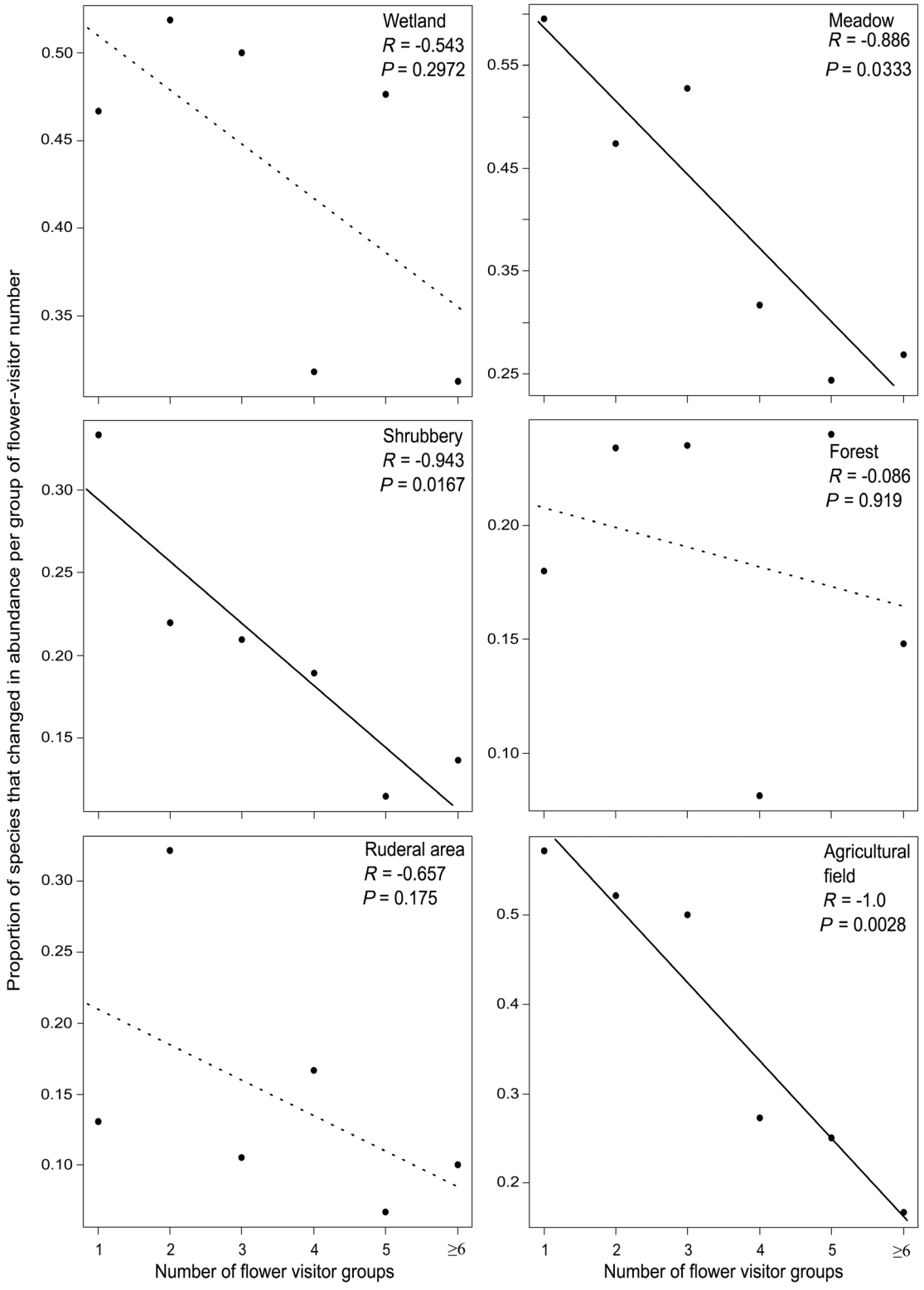

FIG. 3. Spearman correlations between the number of flower-visitor groups per plant species and the proportion of species that changed in abundance per group of flower-visitor number. Significant correlations ($P < 0.05$) are shown with solid lines and non-significant correlations are shown with dotted lines.

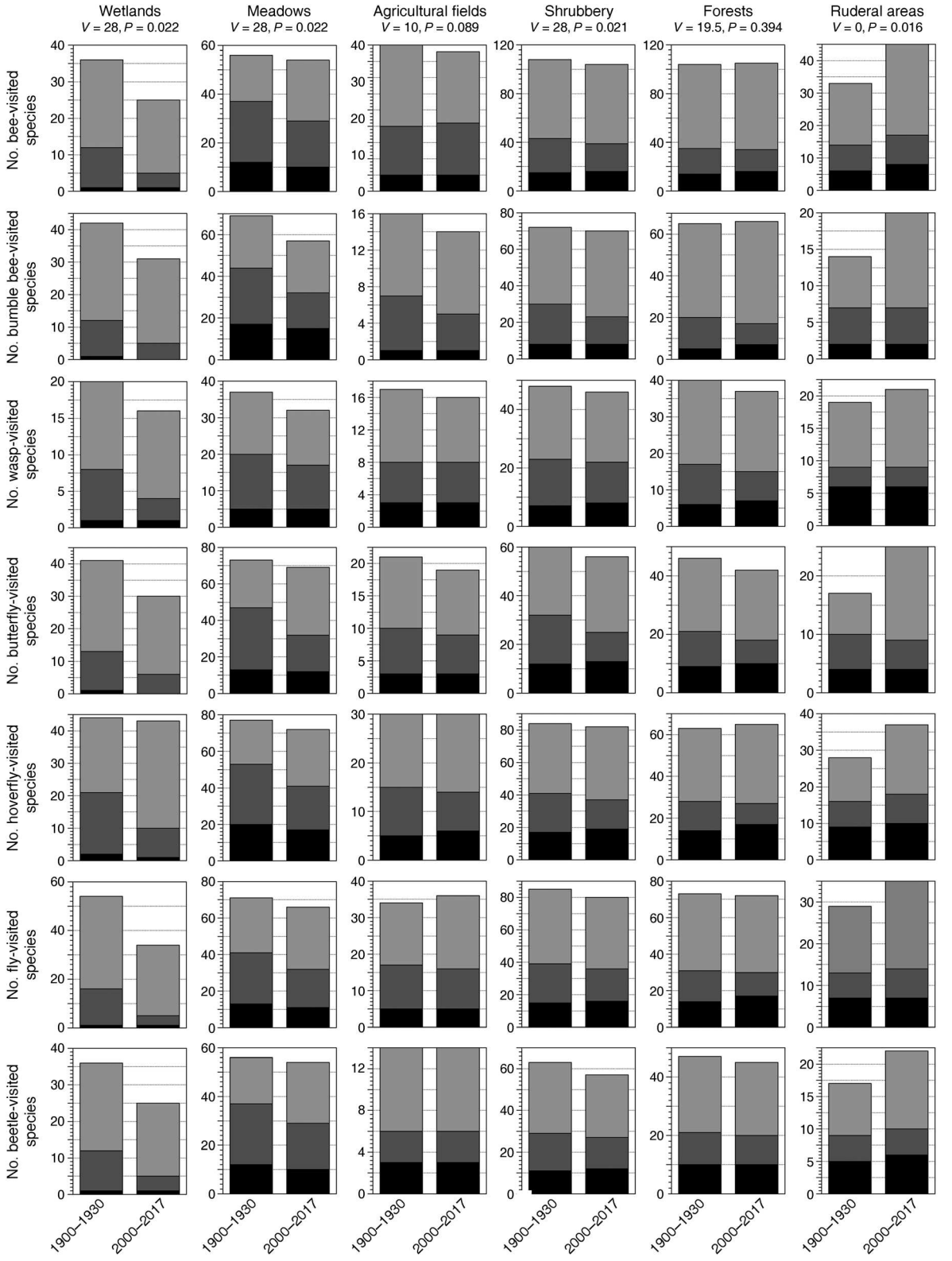

FIG. 4. Comparison of the number of abundant species (black, very common; dark gray, common; light gray, locally common) as a sum between historical and current data in the different vegetation types, separated by flower-visitor group. *P* values indicate results of paired Wilcoxon tests. *V* indicates sum of ranks assigned to the differences with positive sign.

(Rollin et al. 2016). The second vegetation type with significant reductions in food plant availability is wetland. In contrast to in agricultural fields, the overall availability of food plants, which typically occur in wetlands decreased for all groups of flower visitors because of the massive loss of wetland area (□90% loss in the canton of Zurich; Wohlgemuth et al. 2020), which affected the abundance of wetland plants and thus all groups of flower-visiting insects.

In other vegetation types, such as meadows and forests, we also documented decreases in food plant abundances, but these trends were mostly not significant (Fig. 2). This may, at least partly, be a result of our coarse abundance categorization and should not be taken as an indication that such habitats did not experience ecologically relevant changes in food plant abundances. Species composition in meadows changed considerably over large areas, and species richness massively decreased due to intensive fertilization and higher frequency of mowing in most of the grassland area (Lachat et al. 2010, Gattlen et al. 2017). However, many typical meadow species still thrive in many places in the landscape and were thus categorized as largely unchanged in abundance. Some of these species are slightly shade tolerant and survive in habitats adjacent to former grassland, e.g., at forest edges or in shrubbery (Bornand et al. 2016). Even after the exclusion of all species occurring in nutrient-rich meadows, this pattern remained constant for all groups of plants except those visited by butterflies, which underwent nearly significant decreases in abundances. In forests, food plant abundances decreased, which relates to changes in forest management from simple coppice and coppice with standards to high forests (Bürgi 1999), leading to denser stands and fewer flowering plants in the herbaceous vegetation (Schiess and Schiess-Bühler 1997, Wohlgemuth et al. 2002).

In addition to the general decrease in food plant availability for flower-visiting insects, we found that more specialized plant species, i.e., species with few groups of flower visitors, have always been comparatively rare and have decreased more strongly in abundance than plants with many groups of flower visitors. These more specialized plant species are mostly (about 70%) visited by specialized groups of flower visitors such as bees, bumble bees and Lepidoptera. One may argue that this differential decrease can be explained by different habitat associations among plant species with different degrees of pollinator specialization: plant species with high pollinator specialization may be overrepresented in vegetation types in which food plants generally declined more strongly, such as wetlands. However, we found that the distribution of vegetation types in each of the specialization categories did not differ significantly from the distribution of vegetation types in the entire data set. The strong decline of plant species highly adapted to few pollinator species (such as *Aconitum* sp. pollinated by bumble bees) may thus at least partly be linked causally to the drastic population breakdowns of their mostly specialized groups of flower visitors and vice versa (Biesmeijer et al. 2006, Kosior et al. 2007, Nilsson et al. 2008, Wallisdevries et al. 2012). Therefore, besides habitat loss, the decline in pollinator and flower abundance is a severe threat for specialized pollination mutualisms, as well as for the species involved (Weiner et al. 2014).

In addition to the decline in food plant availability, we detected a strong homogenization of the food plant assemblages in all vegetation types except ruderal areas, where we found the opposite pattern (Fig. 4). This decline in the number of dominant food plant species is mostly shaped by a decrease in the number of historically common and locally common species. However, the number of very common species was fairly constant, whereas the number of rare and very rare species increased strongly in the current vegetation. This homogenization of the food plant communities not only reduces the absolute availability and diversity of food sources for individual groups of flower visitors in different vegetation types, but may also lead to temporal shortages of food for some groups of flower-visiting insects, especially the more specialized groups. Such homogenization may thus be interpreted as a major threat to pollinator diversity (Fründ et al. 2010, Weiner et al. 2011, Carvalheiro et al. 2013).

The phenological changes in food plant abundance differed between vegetation types and groups of flower-visiting insects. In wetlands, the largest changes in the abundance of food plants for specialized groups, such as bees, bumble bees, and butterflies, occurred in May, followed by the largest changes for generalized groups, such as flies and hoverflies, in July. This pattern is in congruence with phenological abundance and diversity patterns of flower-visiting insect groups in seminatural habitats in Europe, with specialized visitors peaking earlier in the year than generalists (Balfour et al. 2018). Leong et al. (2016) found that in strongly human-altered landscapes, such as agricultural fields, the peak of bee abundance has shifted over time from early towards late summer. This pattern was explained by a decrease in food plant availability in agricultural fields in late spring and early summer resulting from intensive management (Leong et al. 2016). The results of our study provide empirical support that this gap in flower availability is based on a differential decrease in food plant abundances in early summer, probably due to specific land-use techniques that most strongly affect plant species flowering at this time of the year.

The Swiss Red Lists for bees/bumble bees and butterflies indicate a drop of 50–60% in the species abundances in both groups, owing to habitat loss induced by land-use change and the massive application of fertilizers and pesticides in agricultural land (Cordillot and Klaus 2011). For Diptera, a red list is lacking. Compared with the decreases in insect abundance, the decreases in their food plant species by 28–33%, as demonstrated here, appears less severe at first glance. However, food plant

shortages are most distinct during late spring/early summer in wetlands and agricultural fields. Therefore, we conclude that the decrease in food plant abundance may be one of the most important factors contributing to the reduction in flower-visiting insects (Carvell et al. 2006, Fitzpatrick et al. 2007, Nilsson et al. 2008, Bates et al. 2011, Wallisdevries et al. 2012, Scheper et al. 2014, Schleuning et al. 2016). The loss of flower-visiting insects particularly impacts plant species dependent on outcrossing by pollinators (Biesmeijer et al. 2006). Suitable habitats need to be extended to reverse the negative trend of loss of specialized plant species and their characteristic flower-visiting insects. In addition, reestablishment of selected plant species adapted to few pollinator species can bring back some of the rare, specialized insects (Noël et al. 2011).

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